Annual Variation in Larval Amphibian Populations Within a Temperate Pond

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ABSTRACT

This study reports the results of a four year monitoring program of larval amphibians from a single pond located in the eastern United States. Striking year to year population variation occurred in terms of (1) population size, (2) larval recruitment, and (3) habitat use. The present data base precludes isolation of cause and effect relationships in the population dynamics of larval populations. Any given kind of larval amphibian population variation is the simultaneous interactive result of several causes.

Basic to an understanding of the functioning and dynamics of amphibian communities is a knowledge of the kinds and intensities of year-to-year variation in larval populations. Surprisingly, little basic information is available for larval amphibian communities. Most studies of variations in amphibian life history patterns have focused on the adult phase, treating the larval phase as a kind of "black box." The number of quantitative studies analyzing larval population dynamics at the community level can be counted on the fingers of one hand. The most important of these studies is from a two-species amphibian community in British Columbia, Canada (Calef, 1973). The present study was undertaken with the purpose of gathering basic information on year-to-year variability in larval populations from a diverse temperate amphibian community.

The results of a four-year monitoring program of larval amphibians from a single pond located in the coastal plains of Maryland are reported herein. The study site is a large pond which rarely dries up completely. Data from the first two years have been analyzed previously with respect to habitat partitioning (Heyer, 1976). The patterns of larval occurrence of growth stages and microhabitat overlap are similar for all years of the study and are not dealt with further (see Heyer, 1976, for first two year's results).

Methods and Materials

Minimum and maximum daily temperatures and daily rainfall were taken from records kept by the Environmental Sciences Program of the Smithsonian Institution at the Chesapeake Bay Center for Environmental Studies, near Edgewater, Anne Arundel County, Maryland. Pond water temperatures were recorded when weekly samples of larval amphibians were taken through the spring, terminating at the end of June for four successive years. Three dipnet sweeps were taken each week during the sampling period: a surface, midwater, and bottom sample. The pond, together with details on how the sweeps were taken and the disposition of the larval samples through identification, are described elsewhere (Heyer, 1976). The basic data set analyzed herein consists of the numbers of larvae of the species taken in each sweep sample each week. The raw data comprise an adjunct appendix which is available from the author on request. This data set is supplemented with field notes recorded each week during the sampling period.
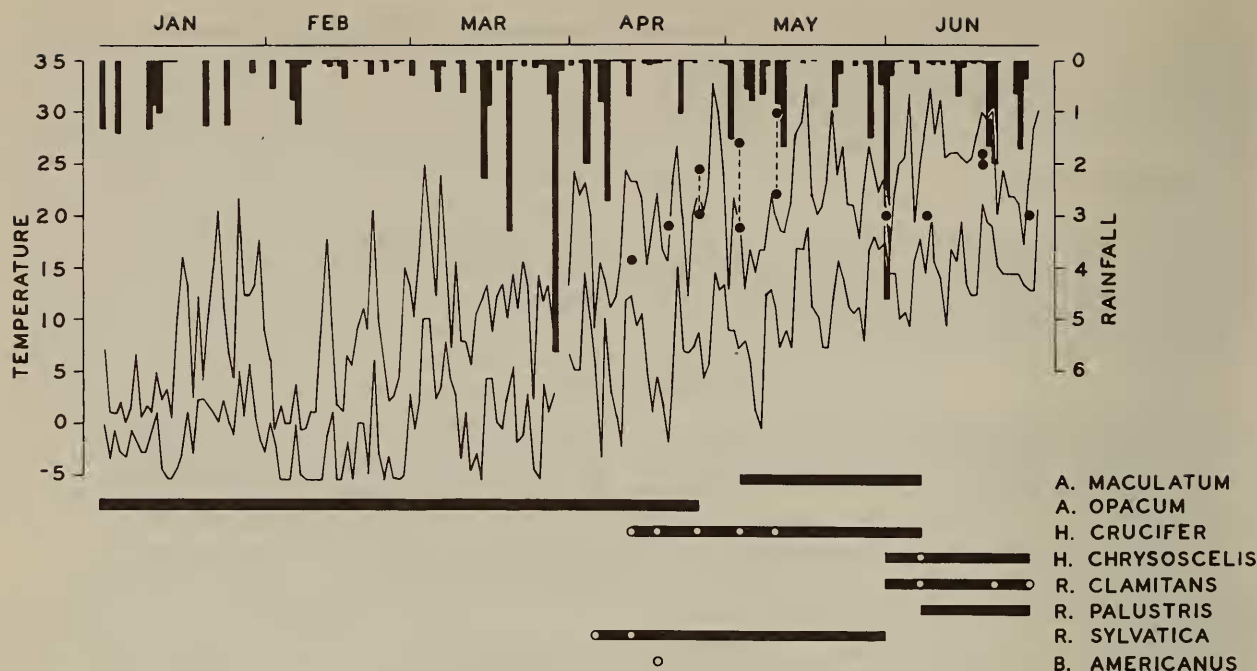
Fig. 1. Climatic and larval occurrence patterns for the first 180 days of 1974. Rainfall in cm, maximum and minimum temperatures in degrees Celsius. Solid circles equal surface water temperatures taken in shade and sun, afternoon readings. If only a single water temperature, sky was overcast. Dark horizontal bars equal presence of free swimming larvae captured in nets. Presence of *A. opacum* assumed from 1 January to first sampling date. Open circles equal presence of eggs, hatchlings, or Gosner (1960) stage 25 or 26 tadpoles and represent larval recruitment (data not gathered for salamanders).

Results of the four-year study differ slightly from results of the previous two-year study (Heyer, 1976) for three reasons. The first is that *Rana palustris* larvae were not identified until the third year's sample was being processed. In the previous report, the *Rana clamitans* samples contained *Rana palustris*. The earlier collections were re-examined and identifications were corrected for the present study. Second, a single sample of 296 *Bufo americanus* larvae which had just hatched from their egg string was included in the previous analysis. These are excluded from this study as they represent data on egg placement rather than larval habitat use. Third, *Acris crepitans* was not analyzed as the species was taken rarely in the pond (data are included in the total numbers of larvae category as used in the niche breadth measures, however).

Results and Analyses

Climate, Larval Occurrence, and Numbers of Individuals.—Figures 1–4 show the relationship of the climate parameters of temperature and rainfall with occurrence of eggs, recently hatched larvae and older larvae. Recently hatched larvae (Gosner, 1960, stages 25–26) are included to provide information on population recruitment.

The numbers of larvae sampled each year are presented in Table 1. Because sampling techniques were the same over the four-year period, the numbers of larvae sampled reflect changes in population size over the four years.

It is clear that several biotic and abiotic factors varied during the four-year study. There was considerable variation in the intensity of winter cold conditions, in the timing and intensity of warming trends in the spring, and in the amount and distribution of rainfall. The time that larval populations were in the pond varied from year to year, as did the length of the larval recruitment period for those species with a long breeding season (e.g., *Hyla crucifer*), and the total larval biomass.
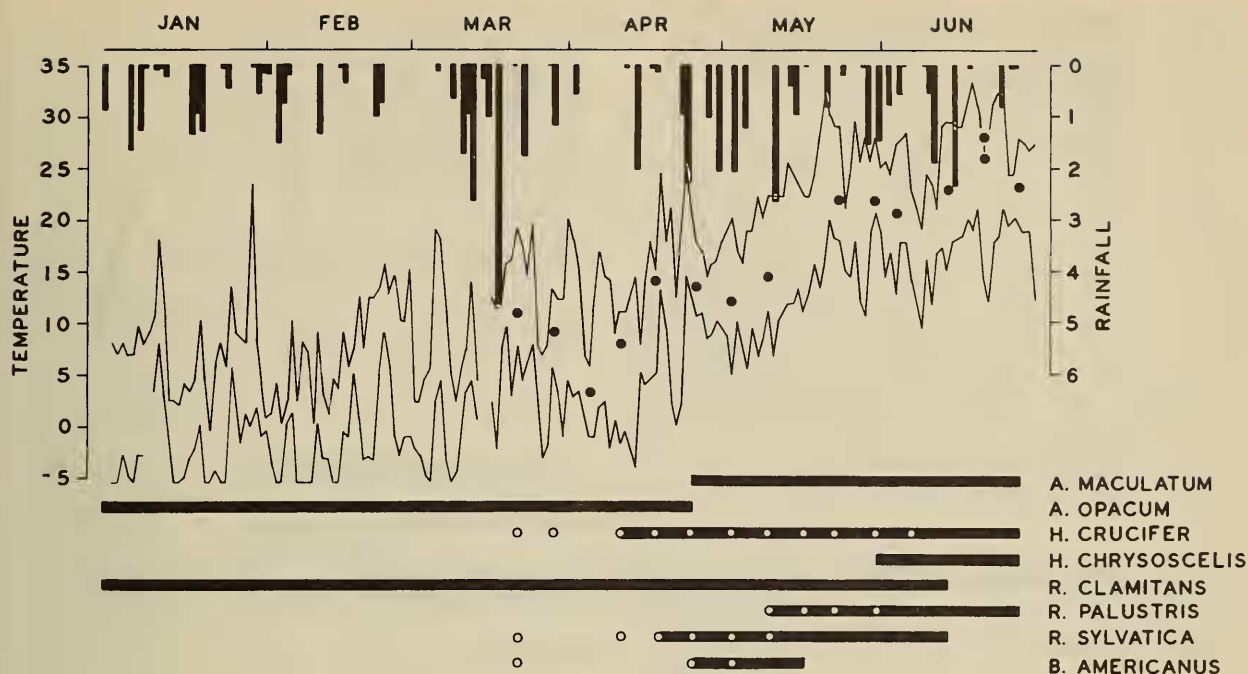
Particular weather patterns unques-

Fig. 2. Climatic and larval occurrence patterns for the first 180 days of 1975. Legend as for Fig. 1 except water temperatures taken in morning; presence of *A. opacum* and *R. clamitans* assumed from 1 January to first sampling period.

tionably account for two instances of larval dynamics. The extremely cold winter of 1977 killed all overwintering *Ambystoma opacum* larvae and greatly reduced the population of overwintering *Rana clamitans* larvae. Keith Berven (pers. comm.) found many *Rana clamitans* larvae trapped in ice on the pond in

the early spring of 1977. Other weather patterns may account for variations in other larval populations (e.g., *Rana sylvatica*), but other relationships are not as clear or obvious as those discussed for *Ambystoma opacum* and *Rana clamitans*. Certain other probable cause-and-effect relationships are discussed below.
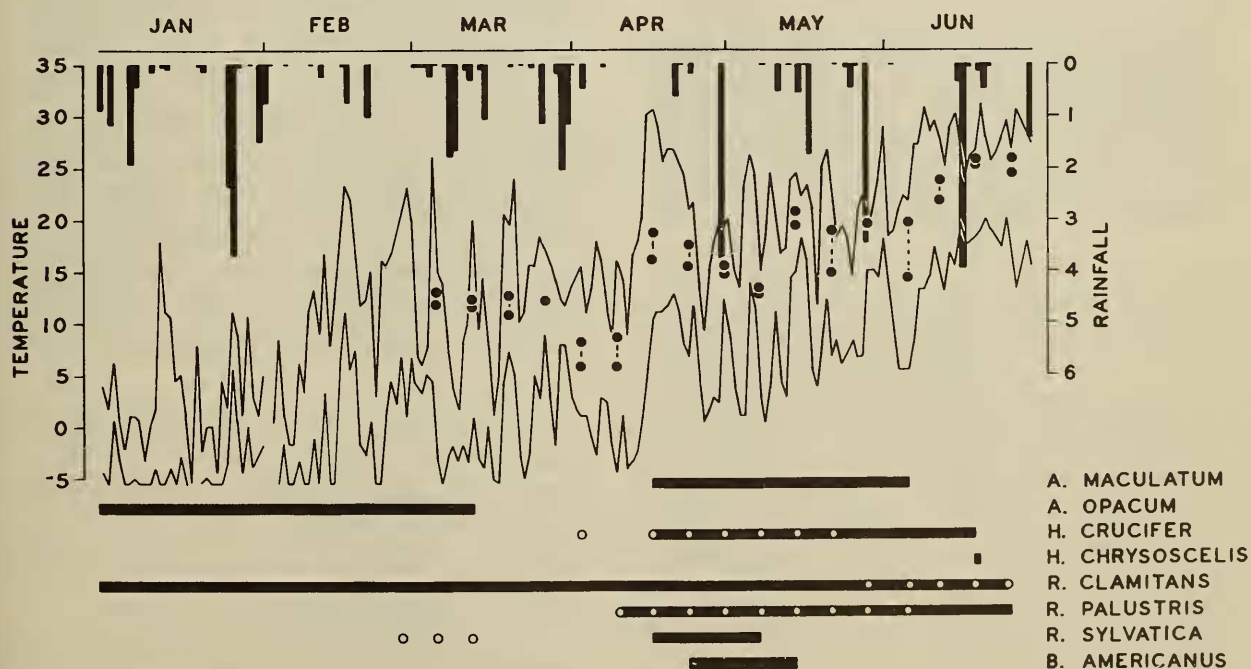

Fig. 3. Climatic and larval occurrence patterns for the first 180 days of 1976. Legend as for Fig. 2.
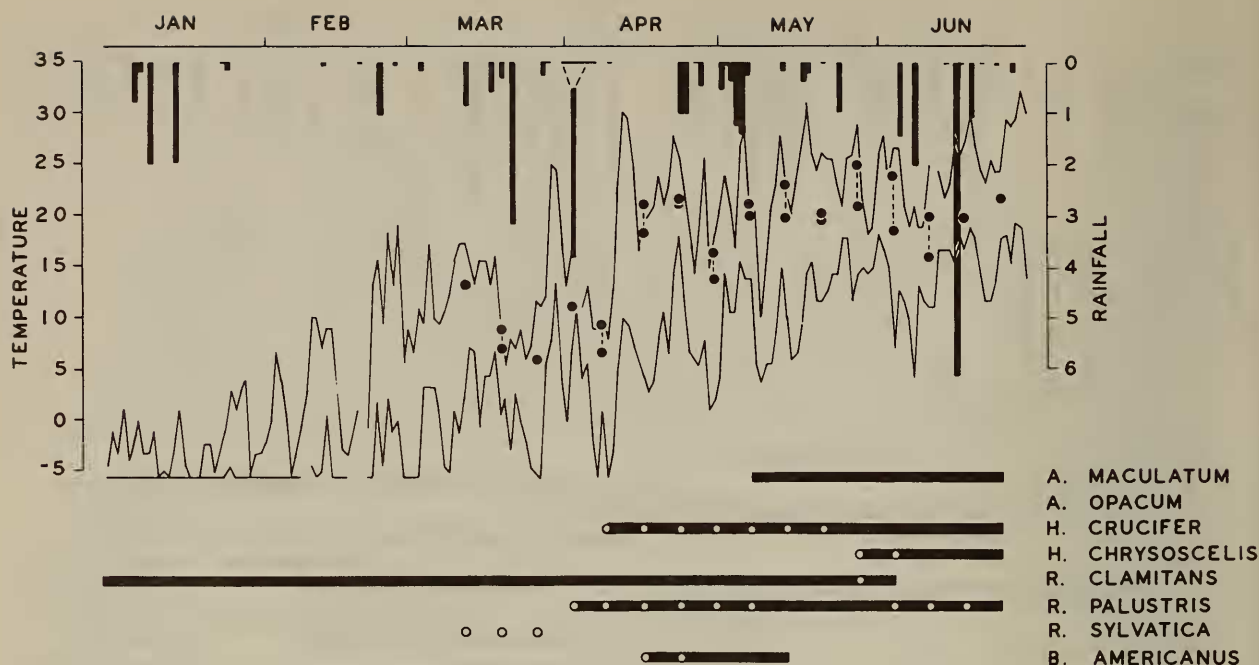
Fig. 4. Climatic and larval occurrence patterns for the first 180 days of 1977. Legend as for Fig. 2 except rainfall for first five days of April combined; presence of *R. clamitans* assumed from 1 January to first sampling date.

Habitat Use.—Larval Distribution in Sweep Types.—Individual species of larvae are not equally distributed among sweep types (Table 2). The three sweep types sampled different microhabitats within the pond. The unequal distribution of larvae among sweep types reflects habitat partitioning by the larvae (also see Heyer, 1976).

Microhabitat Breadth.—Another mode of habitat utilization concerns distribution across all microhabitats in the pond. The basic information statistic commonly used to compare species use of a habitat is the formula for niche breadth:

$$B_j = \sum_i p_{ij}^2,$$

where B_j is habitat breadth and p_{ij} is the proportion of occurrence of species j in sweep i (modified from Levins, 1968).

The habitat breadths calculated from the summarized sweep data of Table 2 are presented in Table 3. The resultant values (Table 3) give an overview of how the three microhabitats (three sweep types) were used from year to year by the entire species assemblage. Most of the species used little of the sampled habitat, but a few species used much of the sampled habitat. Considerable year to year variation occurs among the three sweep types.

In summary, three kinds of year to year larval populational variation account for the variation discussed and documented above. These, ranked in what are believed to be the decreasing order of importance are:

1) Population size. Variation in the number of larvae of each species from year to year.

Table 1.—Numbers of Larvae Sampled.

	1974	1975	1976	1977
A. maculatum	17	134	80	20
A. opacum	12	4	10	0
H. chrysoscelis	26	26	2	21
H. crucifer	634	1884	1295	754
R. clamitans	12	58	60	20
R. palustris	2	107	488	377
R. sylvatica	191	79	5	0
B. americanus	0	480	345	86
Totals	884	2790	2285	1284

2) Larval recruitment. Variation in the time at which hatchlings are incorporated into the populations, as well as how many times they are incorporated each year.

3) Habitat use. The differential utiliza-

Table 2.—Total Numbers of Larvae Sampled by Sweep Type.

	S	M	B	X^2
A. maculatum				
1974	11	2	4	7.88*
1975	59	28	47	10.94**
1976	48	27	5	34.68***
1977	14	3	7	7.75*
A. opacum				
1974	6	3	3	—
1975	0	1	3	—
1976	2	6	2	—
1977	0	0	0	—
H. crucifer				
1974	530	46	58	721.11***
1975	891	566	427	180.60***
1976	1001	136	158	1126.92***
1977	642	40	72	912.90***
H. chrysoscelis				
1974	6	17	3	12.54***
1975	3	12	11	5.62
1976	1	1	0	—
1977	20	1	0	36.29***
R. clamitans				
1974	3	1	8	—
1975	11	10	37	24.24***
1976	24	12	24	4.80
1977	8	4	8	1.60
R. palustris				
1974	0	1	1	—
1975	0	63	44	58.56***
1976	1	253	234	242.12***
1977	32	151	194	112.08***
R. sylvatica				
1974	7	130	54	121.00***
1975	6	34	39	24.03***
1976	2	2	1	—
1977	0	0	0	—
B. americanus				
1974	0	0	0	—
1975	4	433	43	703.46***
1976	1	207	137	190.82***
1977	6	60	20	54.79***

* = Significant at 5% level, ** at 1% level, *** at 0.1% level. S = surface sweep, M = midwater sweep, B = bottom sweep. X^2 testing hypothesis S:M:B.

Table 3.—Habitat Breadths, Based on Summed Sweep-Type Occurrences.

	1974	1975	1976	1977
A. maculatum	0.01	0.01	0.01	0.01
A. opacum	0.01	0.01	0.01	0
H. chrysoscelis	0.01	0.01	0.01	0.01
H. crucifer	1.14	1.50	0.98	0.87
R. clamitans	0.01	0.01	0.01	0.01
R. palustris	0.01	0.01	0.33	0.76
R. sylvatica	0.64	0.01	0.01	0
B. americanus	0	0.14	0.16	0.06

tion of microhabitats by each species from year to year.

Interactions among these three kinds of variation produce the results seen in year-to-year variation of habitat breadths (Table 3).

Discussion

Two observations that contributed to the observed variation are difficult to explain. The first is the collection of *Bufo americanus* larvae as they were hatching in 1974, but the lack of subsequent larval captures of this species for 1974. The second is the absence of *Rana sylvatica* larvae in the 1977 samples, despite the fact that *Rana sylvatica* was known to breed that year, the egg masses were as abundant as in previous years, and the eggs hatched. There were no obvious instances of greater egg mortality in 1977 than observed in other years, nor were predators observed at the egg masses. A possible explanation is that the 1977 larvae were killed by heat. The temperature of 30 March was unseasonably warm (Figure 4), and the hatchling larvae have an upper thermal temperature tolerance of about 35°C (Zweifel, 1977). On 30 March, the hatchlings likely were still congregated around the egg masses. The eggs were laid in shallow water exposed to direct sunlight, a situation where water temperature sometimes exceeds the maximum air temperature (as in Figure 1). Unfortunately, no temperature readings of the water were taken at the egg mass site on 30 March nor is the degree of

larval dispersal known, so this explanation must remain speculative.

The remainder of this discussion focuses on the year-to-year larval variation, the probable sources of the variation, and the interactions between kind and source of variation. The purpose of the discussion is an attempt to understand what annual variation means in the larval amphibian community studied. Although discussion centers upon the study community itself, much of the interpretation should be valid for larval amphibian communities in general. Data from this study are integrated with results from other studies. In attempting to present a complete discussion, some assumptions are made where no data are available; such assumptions lack literature citations.

Three major modes of year-to-year larval population variation are documented above: population size, recruitment, and habitat use. Larval recruitment reflects the interaction of three components: (1) egg deposition, that is, when and how often the adults deposit egg masses; (2) egg and embryonic mortality; and (3) embryonic development, that is, the amount of time involved from egg deposition to hatching into a free swimming larva. For purposes of discussion, these three components are treated separately. Two other expressions of larval variation not examined in this study, but potentially important are: the time from hatching to metamorphosis, and the size of larvae at metamorphosis. These seven kinds of variation are likely the most important affecting the larval community under study. The relative importance of these kinds of variation are thought to be: (1) population size (egg number), (2) egg deposition, (3) egg and embryonic mortality, (4) embryonic development, (5) size at metamorphosis, (6) time from hatching to metamorphosis, and (7) habitat use.

The major sources of year to year larval population variation are (no ranking order intended):

1) Physical-climatic factors. The interaction of rainfall, temperature, and photoperiod likely are sufficient descriptors.

2) Number and breeding pattern of adults. More variation would be expected in non-territorial species (e.g., *Hyla crucifer*) than in territorial species (e.g., *Rana clamitans*). More variation would be expected in species with a prolonged breeding season (e.g., *Hyla crucifer*) than in species with a single egg deposition pattern (e.g., *Rana sylvatica*).

3) Food resources. The two species of salamanders probably feed on the same kind of food, aquatic invertebrates and tadpoles. The six species of tadpoles are all scraping and chewing feeders and likely feed on detritus, algae, epifauna, and plankton. Previous studies suggest larvae with similar mouthparts would be feeding on these kinds of food (e.g., Heyer, 1973), but no feeding data were gathered in this study.

4) Predators. Potential predators of salamander larvae in the study pond include other salamander larvae and aquatic insects. Tadpole predators include salamander larvae and aquatic insects. No quantitative data on predation were obtained in this study.

5) Intra-specific and 6) inter-specific competition among larvae. No direct data for these interactions were taken in this study.

Neither the expressions of variation nor their sources are independent factors. As one example, habitat use is probably density-dependent, i.e., correlated with population size. Similarly, the number of breeding adults and predators undoubtedly are influenced strongly by physical-climatic factors.

The most important observation to be made is that each causal factor finds expression in more than one kind of variation, and conversely, that each mode of variation, save one, has more than one cause (Table 4). The one exceptional mode is variation in embryonic development. This is largely influenced by physical climatic factors, ignoring genetic variation in developmental time. Genetic

Table 4.—Sources of Variation Affecting Various Parameters in Larval Amphibian Populations.

Parameter	Physical-climatic factors	# & breeding pattern of adults	Food re-sources	Pred-ators	Intra-specific compe-tition	Inter-specific compe-tition
1. Population size	E	×	(×)	×	(×)	(×)
2. Egg deposition	×	×				
3. Egg and embryonic mortality	×			×		
4. Embryonic development	×					
5. Metamorphic size	×		×		×	×
6. Time from hatching to metamorphosis	×		×		×	×
7. Habitat use	E		×	×	×	×

E = Cause and effect documented in this study, × = cause and effect documented or presumed from other studies, (×) cause and effect presumed to be of minor importance.

variation, while evolutionarily important, should not be an important factor over ecological time as considered in this study. The amount of yolk stores also affects developmental time. Variation in yolk stores within eggs of each of the study pond species is not known, but probably would add only a day or two of variance at most in hatching time as all study pond species have relatively little yolk in each egg. Other possible causes of variation in embryonic development time, such as oxygen concentration, although probably not important for the study pond populations, could be important at other sites. Causal factors are now discussed in terms of the modes of variation they produce, with documentation from this and other studies.

The only source of variation that affects all parameters considered here is the category "physical-climatic" factors. This study documents the apparent effect of a severe winter on populations of *Ambystoma opacum* and *Rana clamitans*. Another common physical-climatic factor affecting population dynamics is the drying up of temporary ponds (Heyer, 1973; Wiest, 1974). Physical-climatic factors are very important in determining when eggs are deposited. The most thorough analysis of this phenomenon is Savage's (1961) study of variation in egg deposition dates in the frog *Rana temporaria*. Savage (1961) found that aspects of temperature, rainfall, photoperiod,

altitude, longitude, and latitude could be used to build a multiple correlation co-efficient mathematical model that accounted for 50% (r^2) of the total variance of observed spawn dates for *Rana temporaria*. Because of the immense volume of data required to perform an adequate analysis of this sort, it is unlikely that Savage's study will ever be repeated for another amphibian species. Egg mortality due to heavy rains, ponds drying or freezing is well known (e.g., Heyer, 1973), as is the relationship between temperature and variation in embryonic development time (e.g., Lillie and Knowlton, 1897; Moore, 1939). The present study demonstrates that a harsh winter can affect habitat use by removing one species from the habitat. Temperature also is known to affect the time from hatching to metamorphosis as well as size at metamorphosis (e.g., Herreid and Kinney, 1967).

The number of breeding adults determines the maximum number of larvae in the pond. The number of breeding adults also might affect variation in timing of egg deposition, especially in species with extended breeding seasons. If adult population densities are high, eggs should be laid on more days than if adult population densities are low.

Food resources could be so limiting that some individuals actually died from starvation, thereby affecting variation in population size. This is probably a rare situation, as most temporary ponds likely

have a flush of energy input with a resultant algal bloom that is cropped by the tadpoles. Distribution of food resources could affect habitat use if the food resources were patchily distributed. Food resources affect the time from hatching to metamorphosis as starved tadpoles continue to live but do not grow (e.g., Calef, 1973). Food resources also affect the size of the larvae at metamorphosis.

Predators have a direct effect on larval population size due to feeding on eggs and free swimming larvae (e.g., Brockelman, 1969; Calef, 1973). Predators also could have an effect on habitat partitioning, if predators occurred more frequently in some microhabitats and not in others. At the study pond odonate naiads were present in the microhabitats sampled by the surface and bottom sweeps, but not in the midwater sweep microhabitat. Inferential support for predators having an effect on larval amphibian habitat use is found in Heyer, McDiarmid, and Weigmann (1975) and Heyer (1976).

Intraspecific competition can have an effect on population size in the case of cannibalism resulting from competition for food, a possible explanation for the documented cases of cannibalism in *Scaphiopus* (Bragg, 1964). The results of intraspecific competition are not usually this drastic, however. Experimental studies have demonstrated the effects of intraspecific competition on time from hatching to metamorphosis (e.g., Brockelman, 1969). As intraspecific competition has been demonstrated in experimental studies, it is reasonable to assume that competition occurring at high densities would result in the utilization of suboptical habitat by some members of the population. Intraspecific interactions can have a positive or negative effect on size at metamorphosis (e.g., Wassersug, 1973).

The role of interspecific competition is much better understood for salamanders (e.g., Wilbur, 1972) than for tadpoles (e.g., DeBenedictus, 1974). Experimental studies have shown the effects of

interspecific competition on time from hatching to metamorphosis and size at metamorphosis (e.g., Wilbur, 1972). Interspecific competition, if occurring in nature, would be expected to have an effect on habitat use.

The between-year variability outlined above is similar to the variability observed between ponds within a year (Heyer, 1973). Different ponds in a given geographic area have different physical environmental regimes, numbers of breeding adults, food resources, and predators. Because larval population sizes are different from pond to pond, larval competitive interactions among ponds would be expected to differ. Adults of a given amphibian species may be confronted by a variety of breeding ponds which differ extensively in their suitability for breeding and for larval growth. The results of this study indicate that the same sort of marked variability is observed in a single pond over time: this pattern of extreme between-pond and between-year variability puts certain constraints on life history parameters of the amphibians using the environments. Because the larval habitat is unpredictable, a given adult has a better chance of maintaining its genes in the gene pool if it places its eggs in more than one pond or in the same pond for more than one year. The variability demonstrated in this study contrasts with Calef's (1973) study of a two-species permanent pond system in British Columbia, where he found very little variability over a two year period. I believe the British Columbia system is a special ecological situation and the system examined in this study is more typical of larval population dynamics.

The major point of this discussion is that it is virtually impossible to isolate individual cause-and-effect relationships in the population dynamics of naturally occurring larval amphibian populations. For example, variability in size at metamorphosis may reflect the interaction of physical-climatic factors, food resources, and intra- and interspecific competition. An experimental study isolating any one

of these sources of variation could demonstrate variation in size at metamorphosis. Thus, a study which examined competition would demonstrate that competition could explain variation occurring in nature but would not predict whether competition was the only source of larval metamorphic size variation in nature, nor that it was the critical source of variation. A case in point is the attempt to explain the variation seen in larval populations of *Rana palustris* and *R. sylvatica* in the present study. Population sizes of both species were very different from year to year, as was habitat use. Assuming that food resource and predator levels were equivalent over the four years (assumptions needed for simplification to focus on the possible effects of competition, but may in fact not be equivalent), yearly variation in larval populations can be explained in three ways. The first is to invoke interspecific competition. The data in Tables 1 and 3 indicate a trend where the first year is dominated by *R. sylvatica* larvae, the third and fourth years are dominated by *R. palustris* larvae. This could be interpreted as a replacement of one species by the other over time as the result of interspecific competition. However, an equally plausible explanation would be that the variation in population size was due to physical-climatic differences from year to year. Whatever climatic conditions are optimal for *R. sylvatica* larvae are suboptimal for *R. palustris* larvae, and vice versa. Thus, 1974 had climatic conditions optimal for *R. sylvatica* survival and poor for *R. palustris* survival; 1976 and 1977 had climatic conditions optimal for *R. palustris* survival and poor for *R. sylvatica* survival; 1975 had intermediate climatic conditions for both. The fact that about as many *R. sylvatica* eggs were laid and hatched in 1977 as in 1974, lends some support to this explanation. Yet a third plausible explanation would consider the combined effects of climate and competition whereby competitive ability depends on physical conditions. It is impossible to conclusively isolate the factors

of cause and effect of larval population variation in this case, given the data available. Similarly, I think it is impossible to isolate the cause and effect of larval population variation in most, if not all, naturally occurring larval populations, given our present data base.

Conclusions

The larval phase is one part of the amphibian life cycle where the effects of natural selection likely are the greatest. Therefore, it is necessary to understand the kinds and sources of larval population variation in naturally occurring situations to fully understand the amphibian life cycle. The kinds of larval population variations encountered in nature cannot be demonstrated to have simple cause-and-effect relationships. Rather, a given kind of variation is the simultaneous interactive result of several causes.

Experimental studies on larval populations that demonstrate the cause and effect of certain kinds of variation cannot be extrapolated convincingly of field conditions. Experimental studies do lead to a greater understanding of larval population dynamics in nature, however. The experimental manipulation of larval amphibians in a field setting introduced by Brockelman (1969) has been followed by a series of studies, several of which are ongoing, examining the effects of food resources, predation, and intra- and interspecific competition on larval population variation. There is much to be learned from these types of studies, but at our present state of knowledge, we already know more about how larval amphibians live in field pens than in naturally occurring ponds. One of the goals of larval amphibian studies should be to gather basic data on densities and occurrences of larvae in naturally occurring ponds, so that experimental results can be interpreted with greater meaning.

study. Miriam Heyer helped process the larvae in the laboratory. Without their willingness to share their Saturdays with me collecting larvae, the project would not have been undertaken.

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